

EVOLUTION IN THE GENUS *MEOMA* (ECHINOIDEA:  
SPATANGOIDA) AND A DESCRIPTION OF A  
NEW SPECIES FROM PANAMA<sup>1</sup>

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ABSTRACT

The systematics of the echinoid genus *Meoma* is discussed, and a new species of this tropical heart-urchin, *Meoma frangibilis*, is described from the Bay of Panama. *Meoma grandis* is made a subspecies of *Meoma ventricosa*. The genus is traced to a *Macropneustes* ancestor in the early Eocene of Europe.

INTRODUCTION

The discovery of an unknown species of *Meoma* in the Bay of Panama in 1966, during operations aboard the R/V PILLSBURY (Rosenstiel School of Marine and Atmospheric Sciences, University of Miami), prompted a reevaluation of the systematics of the genus *Meoma* Gray. The new species, described in this paper as *Meoma frangibilis*, was initially considered congeneric with *Peripneustes antillarum* (Cotteau) from the Eocene of the Caribbean. Analysis proved, however, that it was closely allied also to *Meoma cadenati* Madsen 1957 from the Recent of West Africa. Examination of specimens of living and fossil species of echinoids which share affinities with the genera *Meoma* and *Peripneustes* indicated that the two genera should be synonymized and provided adequate material for delineating the rates and directions of evolution and the phylogenetic origin of the genus *Meoma*.

Data on the West Indian species, *Meoma ventricosa*, were gathered at the Rosenstiel School of Marine and Atmospheric Sciences in Miami during a study of the ecology and systematics of spatangoids supported by the National Science Foundation (Grant GB 2037) under the supervision of Dr. F. M. Bayer. The holotype of the new species was deposited in the Museum of Comparative Zoology at Harvard University by the Rosenstiel School of Marine and Atmospheric Sciences, through the kindness of Dr. F. M. Bayer. It was collected from the R/V PILLSBURY during operations supported by a National Science Foundation grant (GB 5776). The author

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#### MATERIALS AND METHODS

This paper is divided into three parts: a statistical analysis of large numbers of *Meoma ventricosa* s.s. and *Meoma ventricosa grandis*, with a discussion of the degree and direction of morphological change since the two populations were isolated with the uplifting of the Central American land bridge; the description of a new species of *Meoma* and of *M. cadenati*, and a discussion of the taxonomic status of the four living forms of this genus; and the delineation of affinities of fossil species of *Meoma* back to the Eocene, when the genus apparently evolved from a *Macropneustes* ancestor.

Measurements of the test of *Meoma* were taken using the standard measurements suggested previously (Chesher, 1968). Figure 1 shows the various characters of the test and the method of measuring them. All measurements were made with vernier calipers to the nearest 0.1 mm.

Data from 400 specimens of *M. ventricosa* s.s. were assembled, and more than 100 specimens were used in all analyses. *M. ventricosa* s.s. is represented by specimens from its entire geographic range (Bermuda to Colombia, South America); they range in size from 7 mm to 165 mm in test length. Only 20 specimens (distributed from Colombia to the Gulf of California) of *M. ventricosa grandis* were available for measurements, but the closely similar coefficient of variation between this subspecies and *M. ventricosa* s.s. indicates that the statistical assumptions are valid. Throughout the study, statistical significance is set at the 95 per cent level, using Student's *t* values.

There is only a single specimen of the new species from the Bay of Panama and only two specimens of *M. cadenati* from Africa (only a single specimen was available from Africa for measurements). The second portion of this study relied, therefore, to a large extent on the knowledge gained from the analysis of the populations of *Meoma ventricosa*.

The third portion of the study attempts to show that certain fossil species are more closely related to the concept of the genus *Meoma* than to any other genus. Since reliance must be placed on poorly preserved specimens and old, partially idealized illustrations in the literature, it is impossible to determine means of separating the fossil species from each other or from

the Recent material. The fossil material is, however, sufficient to show affinities with little difficulty. *Peripneustes* (= *Schizobrissus*) *antillarum*, for example, is closely related to *P. clevei*, and the taxonomic problem is one of distinguishing between the two rather than showing them to be congeneric. While it is desirable to follow each species through its genetic lineage, this is not necessary to provide an overall view of the general trend of evolution of the genus and to determine the origin of the genus.

#### ABBREVIATIONS

Abbreviations for the characters of the text are given in the legend to Figure 1. In the text, the abbreviation IA refers to the interambulacra and "per cent TL" indicates that the character discussed is given as a percentage of the length of the test. In the statistical summary of the characters of the test, Log<sub>e</sub> indicates the natural logarithm, C.V. the coefficient of variation, and S.D. the standard deviation.

M.C.Z. refers to the Museum of Comparative Zoology at Harvard University, I.M.S. to the Rosenstiel School of Marine and Atmospheric Sciences in Miami, and U.S.N.M. to the United States National Museum.

#### Genus *Meoma* Gray, 1851

*Meoma* Gray, 1851.—Mortensen, 1951 (complete synonymy).—Fischer, 1966.

*Peripneustes* Cotteau, 1875.

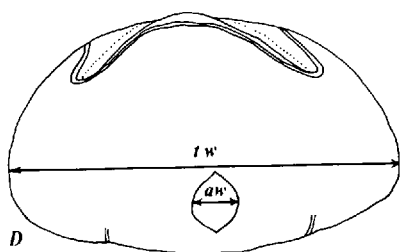
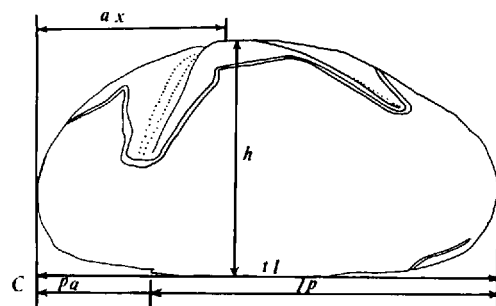
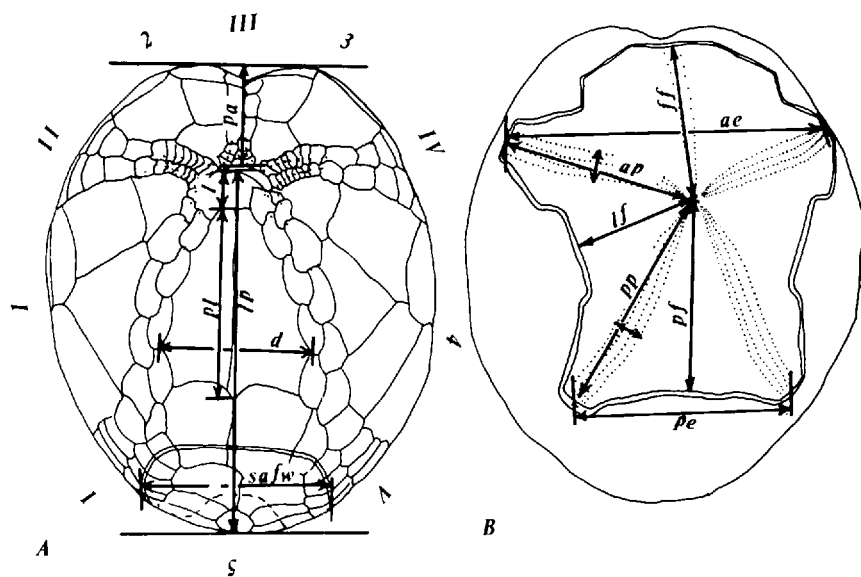
*Schizobrissus*, Mortensen, 1951 (part).

*Macropneustes*, Cooke, 1959 (part).

*Type-Species*.—*Meoma grandis* (= *M. ventricosa grandis*) Gray, 1851.

*Diagnosis*.—Large brissid echinoids with the peripetalous fasciole deeply indented between the paired petals and a sharp reentrant angle in interambulacra 2 and 3; subanal fasciole bilobed, aborally degenerate in adults of one species; anal fascioles absent; notch in anterior portion of test moderate to deep; plastron short (ca. 37 to 45 per cent TL) and broad; epiplastron large, about half the length of the plastron; posterior end of the test obliquely truncate, gently rounded, the anus not visible from above; posterior paired petals of adults long (ca. 40 to 53 per cent TL), narrow, deeply sunken, interporiferous zone narrower than pore zone; four genital pores, apical system ethmolytic, 26 to 46 per cent of the TL from the anterior end of the test; IA not sunken adapically; labrum not past the first adjoining ambulacral plates; no tunneling tube-feet in ambulacrum III.

*Description*.—Table 2 presents the dimensions of the various characters of the test of *Meoma ventricosa* s.s. Thirteen of these characters do not vary significantly among the species of *Meoma*, and can be considered as characters of the genus. These are: the distance from the apical system to the



frontal portion of the peripetalous fasciole, the distance from the apical system to the posterior portion of the peripetalous fasciole, the width of the area enclosed by the subanal fasciole, the width and height of the test and periproct, the distance of the peristome from the anterior or posterior ends of the test, the length of the labrum, the length and width of the posterior petal, and the length of the plastron. Some of these characters are quite variable and others relatively stable (as indicated by the coefficients of variation). Some features of the fascioles are constant in all the species. The peripetalous fasciole is found on plates 6 (3b); 8 and 9 (4a); 9 and 10 (4b); and 12 or 13 (5a). It may also be present on other plates in these same interambulacra. The subanal fasciole is found on plates 3, 4, 5, and 6 (5a), except when the upper portion degenerates in adults of *M. ventricosa*. In ambulacra V, series b, the subanal fasciole is found on plates 6, 7, 8, 9, and sometimes 10.

It is possible to divide the genus into two distinct species groups, a *M. frangibilis*-*M. cadenati* group and a *M. ventricosa* s.s.-*M. ventricosa grandis* group. Of all the characters examined (which include hundreds if subjec-

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FIGURE 1. Definitions of measurements of *Meoma* made with vernier calipers to 0.1 mm, as indicated by the arrows. Abbreviations of other characters are defined, also. *A*, ventral view; *B*, dorsal view; *C*, lateral view; *D*, posterior view. Those measurements shown in *C* are taken with the plastron used as a flat plane of reference and the specimen held against a surface perpendicular to that plane. Lettering: *ae*, distance between the ends of the anterior paired petals; *ah*, height of periproct; *ap*, length of anterior petal from the ocular plate to the last pore-pairs; *apw*, width of anterior petal measured at the widest point from the outer periphery of the two pore-zones; *aw*, width of the periproct; *ax*, distance from the center of the apical system to the anterior portion of the test; *d*, width of the plastron; *ff*, distance from the apical system to the frontal portion of the peripetalous fasciole; *h*, test height; *l*, length of the labrum; *lf*, distance from the apical system to the lateral portion of the peripetalous fasciole; *lp*, distance between the anterior tip of the labrum and the posterior portion of the test; *pa*, distance from the anterior portion of the peristome to the anterior portion of the test; *pap*, number of pore-pairs in the petaloid region of ambulacrum IV, series b; *pe*, distance between the ends of the posterior paired petals; *pf*, distance from the apical system to the posterior portion of the peripetalous fasciole; *pl*, length of the plastron; *pp*, length of posterior petal; *ppfa*, area of the peripetalous fasciole, as determined by multiplying the *ppfl* measurement by the average width of the peripetalous fasciole; *ppfl*, length of the peripetalous fasciole, as measured by "walking" a premeasured set of calipers along its length; *ppp*, number of pore-pairs in the petaloid region of ambulacrum V, series a; *ppw*, width of posterior petal; *pw*, width of the peristome; *safd*, distance from the adoral median section of the subanal fasciole to the periproct; *safl*, length of subanal fasciole; *safw*, width of the area enclosed by the subanal fasciole; *tl*, test length; *tw*, test width; *I*, *II*, *III*, *IV*, *V*, ambulacra; *1*, *2*, *3*, *4*, *5*, interambulacra.

TABLE 1  
CHARACTERS PRESENT (x) AND ABSENT (o) IN THE VARIOUS SPECIES AND  
SUBSPECIES OF THE GENUS *Meoma*

	<i>M. frangi- bilis</i>	<i>M. cadenati</i>	<i>M. ventri- cosa</i> s.s.	<i>M. ventricosa grandis</i>
1. Test thin and fragile in adults	x	o	o	o
2. Anterior paired petal (IV) less than 35% TL	x	o	o	o
3. Peripetalous fasciole on plate 4 of IA 3	x	o	o	o
4. Plastron width (d) greater than 35% TL	o	x	o	o
5. Pores in the posterior petal (y) significantly less than $Y = 11.43 \log_e X - 12.16$ , where $X = TL$ in mm	o	x	o	o
6. Peripetalous fasciole on plate 6 or 7b of amb. III	x	x	o	o
7. Peripetalous fasciole on plate 12 (or less) of amb. IV	x	x	o	o
8. Peristome small, less than 15% TL	x	x	o	o
9. Number of pores in series b of phyllode IV less than 6	x	x	o	o
10. Subanal fasciole degenerate aborally in adults	o	o	x	x
11. Apical system less than 31% TL from the anterior end of the test	x	x	o	o
12. Distance from the periproct to adoral portion of the sub- anal fasciole greater than 24% TL	x	x	o	o
13. Distance from the periproct to the adoral portion of the subanal fasciole less than ver- tical diameter of the peri- proct	o	o	o	x
14. Notch in the anterior portion of the test greater than 6% TL	x	x	o	o

tive data are included) only 14 could be found which differed among the various species. These 14 characters are presented in Table 1. The *M. frangibilis*-*M. cadenati* group differs from the *M. ventricosa* s.s.-*M. ventricosa grandis* group by eight different characters. Whereas five different

characters varied between *M. frangibilis* and *M. cadenati*, only one character differed between the subspecies of *M. ventricosa*. It is evident that *M. frangibilis* has been genetically separated from *M. cadenati* for some time, and that both of these have been separated from the *M. ventricosa* group for a still longer period of time.

The fossil history of the genus is discussed following the description of the living species.

#### KEY TO THE RECENT SPECIES OF THE GENUS *Meoma*

1. Peristome broad (17 to 19 per cent TL) with 8 to 10 oral pores in phyllode IVb; notch in anterior ambitus shallow; peripetalous fasciole on plates 9 to 12, III series b ..... 2
1. Peristome narrow (12 per cent TL) with 5 or 6 oral pores in phyllode IVb; peripetalous fasciole on plates 6 to 7 (IIIb) ..... 3
2. Distance from the adoral portion of the subanal fasciole to the lower portion of the anal system less than vertical diameter of the anal system; dark brown to black pigmentation, coarse tuberculation ..... *Meoma ventricosa grandis*
2. Distance from subanal fasciole to anal system equal to, or greater than, the vertical diameter of the anal system; color light to dark reddish brown, tubercles less coarse ..... *M. ventricosa* s.s.
3. Anterior petal (IV) short, 34 per cent TL, pores in the posterior petal of adult about 42 ..... *M. frangibilis*
3. Anterior petal (IV) long, 45 per cent TL, pores in the posterior petal of adult about 34 ..... *M. cadenati*

#### *Meoma ventricosa ventricosa* (Lamarck, 1816)

Figs. 2, 3, 4, 5; Tables 1, 2, 4

*Spatangus ventricosa* Lamarck, 1816: 29.

*Meoma ventricosa*, Mortensen, 1951: 529, pl. 36, fig. 1, pl. 52, figs. 1, 6, 15 (complete synonymy).—Fontaine, 1953: 8.—Mayr, 1954: 6.—Hyman, 1955: 548, 556, Figs. 174, 175A, 199A, 204B.—Madsen, 1957: 476.—Caso, 1961: 309.—Kier & Grant, 1965: 38, figs. 1-14, pl. 3, figs. 4, 5, pls. 9-13.—Fischer, 1966: U592, fig. 479.2.—Chesher, 1969: 72-110, figs. 1-14.

*Macropneustes ventricosa*, Cooke, 1959: 5, 84, pl. 37, figs. 1-4.

*Material Examined*.—395 specimens, 7 to 165 mm TL, Florida Keys (Alligator and Molasses Reefs) 4 to 50 m.—7 specimens, 115 to 156.5 mm TL, Santa Marta, Colombia, 14 m.—30 specimens, 98 to 164 mm TL, Isla Grande, Panama, 4 to 15 m.—4 specimens, 100 to 114 mm TL, Sandy Point, Abaco, Bahamas, 3.5 m.—3 specimens, 35 to 60 mm TL, Lucaya, Grand Bahama, Bahamas, 3 to 8 m.—4 specimens, 101 to 158 mm TL,

South Bimini, Bahamas, 1 m.—8 specimens, 120 to 162 mm TL, Morgans Bluff, Andros, Bahamas, 3 m.—2 specimens, 111 to 120 mm TL, Whale Key, Berry Islands, Bahamas, 3 m.—20 specimens, 45 to 160 mm TL, Nassau, New Providence, Bahamas, 1 to 3 m.—4 specimens, 119 to 132 mm TL, Elbow Cay, Exuma Island, Bahamas, 11 m.—23 specimens, 121 to 140 mm TL, off Panama City, Florida, depth unknown.—1 specimen, 153 mm TL, North Reef, Bermuda, 8 m; M.C.Z. 8193.—3 specimens, 95 to 148 mm TL, Jamaica; M.C.Z. 3830.

*Diagnosis*.—Aboral portion of the subanal fasciole degenerate in adults, peripetalous fasciole crossing plate 10, 11, or 12 (IIIb); peristome larger than 13 per cent TL, with more than six pores in series b of phyllode IV; color reddish brown to black, distance from lower portion of periproct to adoral portion of subanal fasciole usually equal to, or greater than, the vertical diameter of the periproct.

*Description*.—Table 2 represents a statistical summary of the various characters of the test (as defined in Fig. 1) derived from measurements made on 108 specimens of *M. ventricosa* s.s. from depths of 4 to 60 m at Molasses Reef, Florida Keys. The first section contains data on the characters of the test which do not change their relative proportions markedly over the range of sizes examined (7 to 165 mm in test length). These characters are presented as percentages of the test length. The second and third sections of Table 2 give data on the characters of the test which do change their relative proportion with growth (see Gould [1966] for a recent review of allometry). These characters are represented by the allometric growth-curve formula  $\log_e Y = a + b (\log_e X)$ , where  $Y$  is the length of the character in mm, and  $X$  is the length of the test in mm. The coefficient of correlation,  $r$ , and the standard error of  $Y$  on  $X$ ,  $S_{y \cdot x}$ , are also given. The latter statistic gives an indication of the spread of points about the regression line (Croxtan, 1959). If the scatter plot is normal about the regression line, 68 per cent of the actual values should be within  $\pm 1 S_{y \cdot x}$  (vertically) of the regression line and 95 per cent should be within  $\pm 2 S_{y \cdot x}$ . Since  $S_{y \cdot x}$  is a  $\log_e$  number, it must be added to, and subtracted from, the  $\log_e Y$  value derived for each value of  $X$ . Thus, to derive the length of the anterior petal for a specimen 100 mm in test length,  $\log_e Y = (-1.9238) + (1.2156) (\log_e 100)$ , and  $\log_e Y = 3.6743 \pm 0.073$  and thus,  $Y = 39.2 \pm 3$  mm. About 99 per cent of the specimens would have anterior petal lengths within  $\pm 5.5$  mm of the expected 39.2 mm.

The pore-pairs of the petaloid areas increase as a semi-logarithmic function, and these are given in section 3 of Table 2 as  $Y = a + b (\log_e X)$ , where  $Y$  = pore-pairs, and  $X$  = the test length in mm.

Section 4 of Table 2 summarizes the plate numbers on which the peripetalous and subanal fascioles are found. Loven's system of nomenclature



TABLE 2

STATISTICAL SUMMARY: *Meoma ventricosa* s.s.\*  
(Abbreviations from Figure 1 and section on abbreviations)

SECTION 1: Characters expressed as percentages of the test length					
Character	Mean	S.E.	S.D.	Range	C.V.
tl†	122.57	3.03	31.79	7-165	—
tw	84.86	0.25	2.61	76-96	3.08
h	49.33	0.45	4.70	39-70	9.55
ax	38.81	0.21	2.14	33-46	5.52
pa	17.18	0.19	1.73	14-23	10.08
ff	38.39	0.21	2.00	32-43	5.22
pf	32.76	0.37	3.43	20-42	10.46
lf	23.44	0.21	2.00	17-29	8.55
safw	41.48	0.37	2.31	38-49	5.58
l	7.79	0.09	0.94	6-10	12.05

SECTION 2: Characters ( $Y$  in mm) expressed as  $\log_e Y = a + b(\log_e X)$ ,  
where  $X$  = test length in mm

Character	$a$	$b$	$S_{y \cdot x}$	$r$
ppfl	0.0419	1.2254	0.052	0.99666
ppfa‡	-5.2762	2.3527	0.177	0.98946
ap	-1.9238	1.2156	0.073	0.99323
apw	-2.5658	0.9477	0.159	0.98120
pp	-2.3231	1.3189	0.075	0.99408
ppw	-2.5108	0.9316	0.162	0.97998
ae	-0.9531	1.1137	0.060	0.99803
pe	-1.7592	1.2093	0.057	0.99850
lp	-0.6757	1.0939	0.021	0.99974
pl	-1.3999	1.0969	0.045	0.99679
d	-0.7647	0.9091	0.053	0.99353
vol§	-8.1247	2.9564	0.075	0.98392

SECTION 3: Characters ( $Y$  in pore-pairs) expressed as  $Y = a + b(\log_e X)$ ,  
where  $X$  = test length in mm

Character	$a$	$b$	$S_{y \cdot x}$	$r$
pap	-9.3493	10.4018	2.059	0.93301
ppp	-12.1600	11.4300	2.320	0.92979

SECTION 4: Plates on which fascioles occur

	III b	3		IV a	4		V a	5 a
		a	b		a	b		
Peripetalous fasciole	10-12	5+6 (5-7)	6+7 (5-8)	14-16	8+9 (8-10)	9+10 (8-11)	17-20	13-14
Subanal fasciole	—	—	—	—	—	—	6-10 (6-13)	3 (3-6)

\* N = 108 specimens. Location: Molasses Reef, Florida Keys. Depth: 4 to 60 m.

† Test length in mm.

‡ Area of peripetalous fasciole in mm<sup>2</sup>.

§ Volume of test in ml.

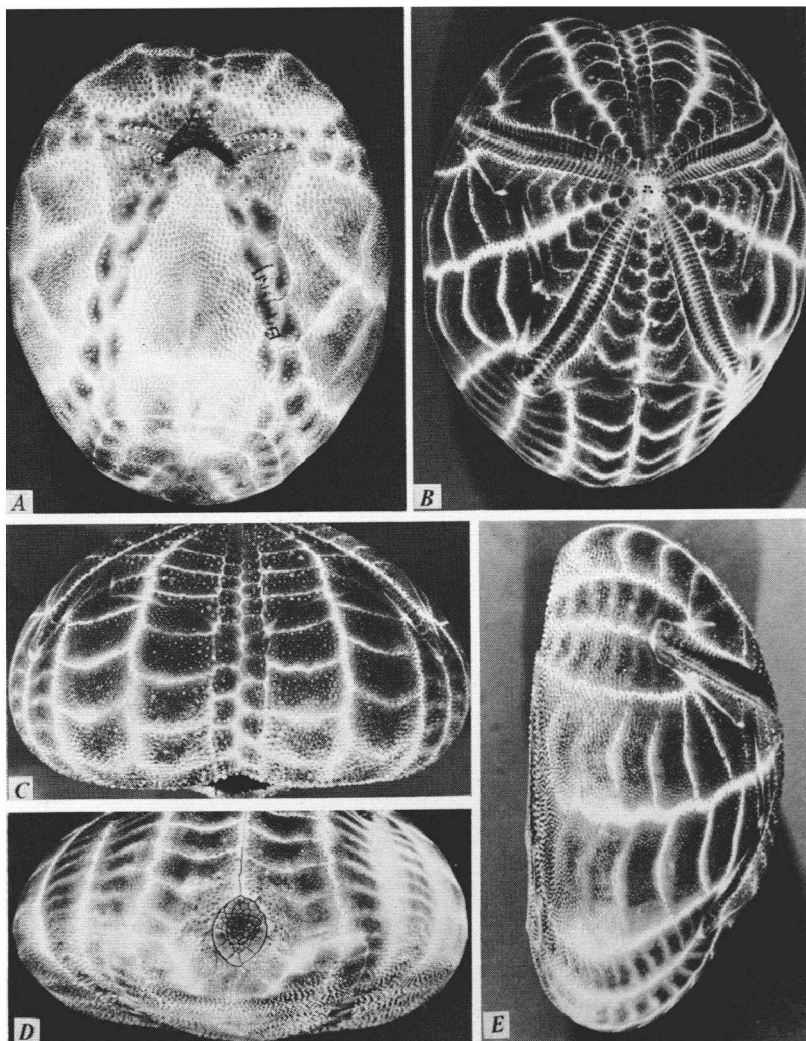


FIGURE 2. *Meoma ventricosa* s.s. (test length 135 mm) with the spines removed and the test partially bleached to show the plate structure. A complete subanal fasciole is present in this specimen. A, ventral view; B, dorsal view; C, anterior view; D, posterior view; E, lateral view.

of the plates (Fig. 1, and discussed by Hyman, 1955) is used, and interambulacral plates were counted using the single plate which inserts to the peristome as plate No. 1 for both series of plates. The plates which have fascioles on them do not change with growth. The numbers in parentheses

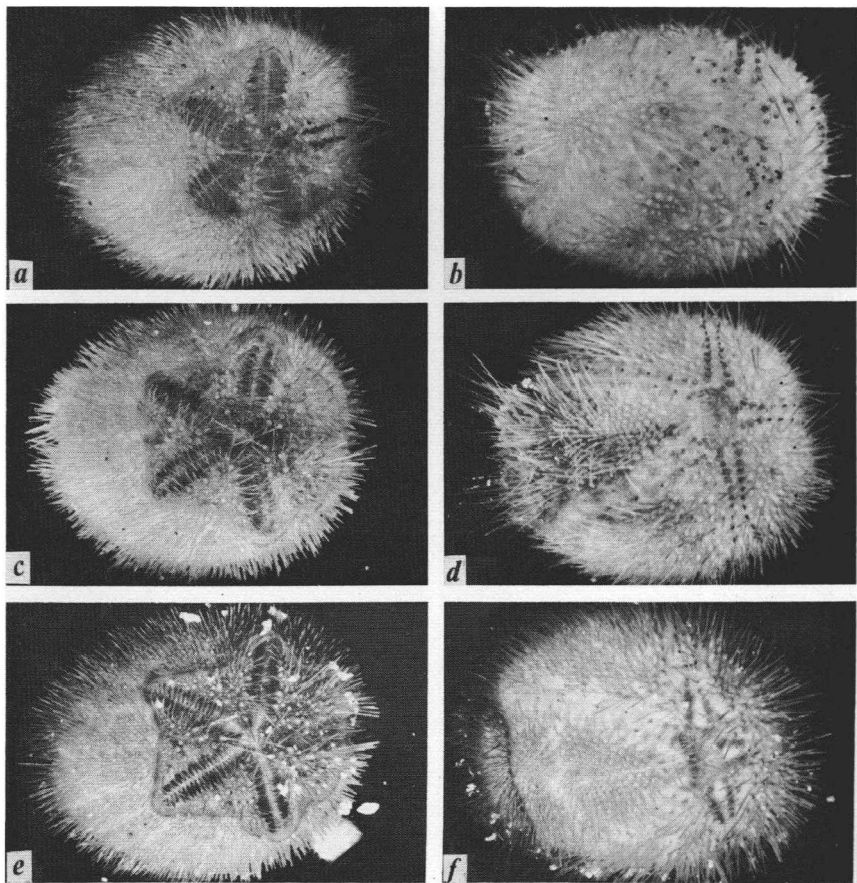


FIGURE 3. Growth series of *M. ventricosa* s.s., photographed alive: *a, b*, dorsal and ventral views of a specimen 18 mm long; *c, d*, same views of a specimen 31 mm long; *e, f*, same views of a specimen 42 mm long.

indicate possible, although uncommon, plate combinations. The number of plates from the peristome to the peripetalous fasciole in ambulacrum IVa may be 14 (22 per cent of the individuals), 15 (36 per cent), or 16 (42 per cent). In ambulacrum Va, the number may be 17 (7 per cent of the individuals), 18 (44 per cent), 19 (38 per cent), or 20 (11 per cent). These numbers are not correlated with size.

Figure 2 shows a specimen of *M. ventricosa* s.s. from Bimini, Bahamas. The specimen is "average" in its dimensions and plate structure. It is abnormal, however, in retaining a complete subanal fasciole. Figure 3 shows

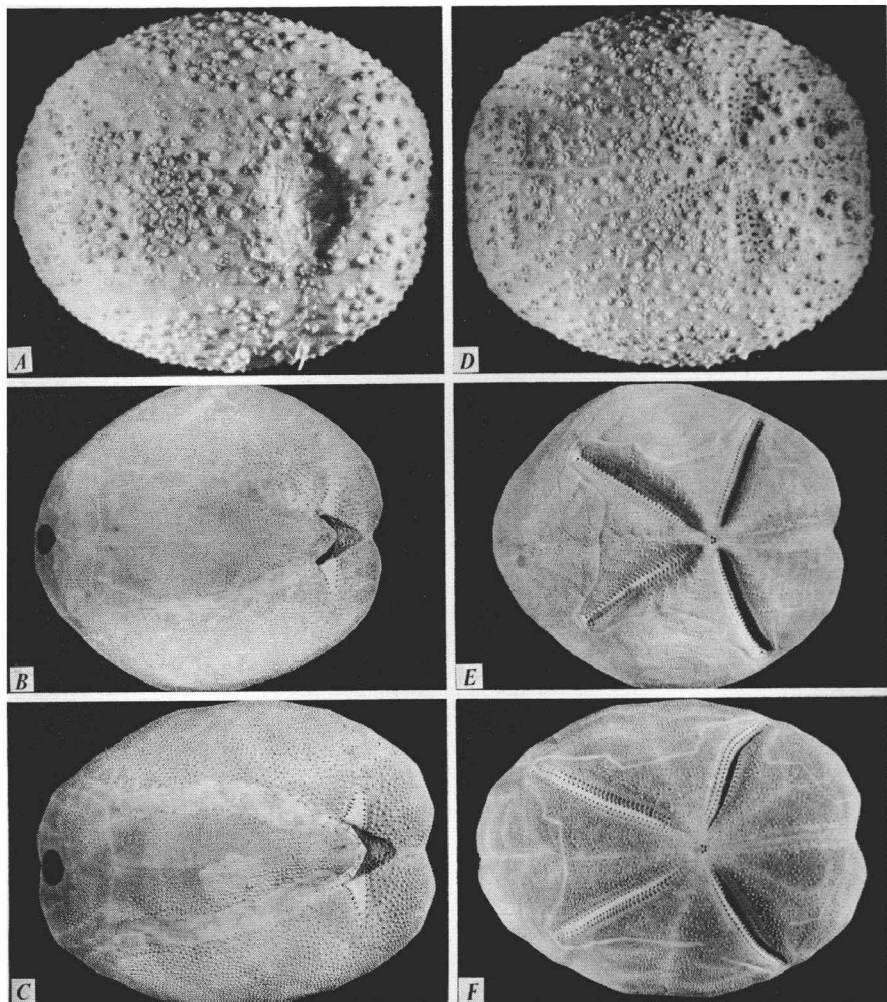


FIGURE 4. Growth and morphological variation in *M. ventricosa* s.s.: A, D, ventral and dorsal views of a specimen 7.0 mm long; B, E, the same views of a highly arched, broad adult 132 mm long; C, F, same views of a low, narrow adult 142 mm long.

a growth series of *M. ventricosa* s.s. with the spines left intact. Various changes in proportions can be seen, particularly the decrease in the relative size of spines and tube-feet and the increase in relative size of respiratory petals. Figures 4 and 5 show a comparison between a juvenile specimen of *M. ventricosa* s.s. and two specimens that show the extremes of adult

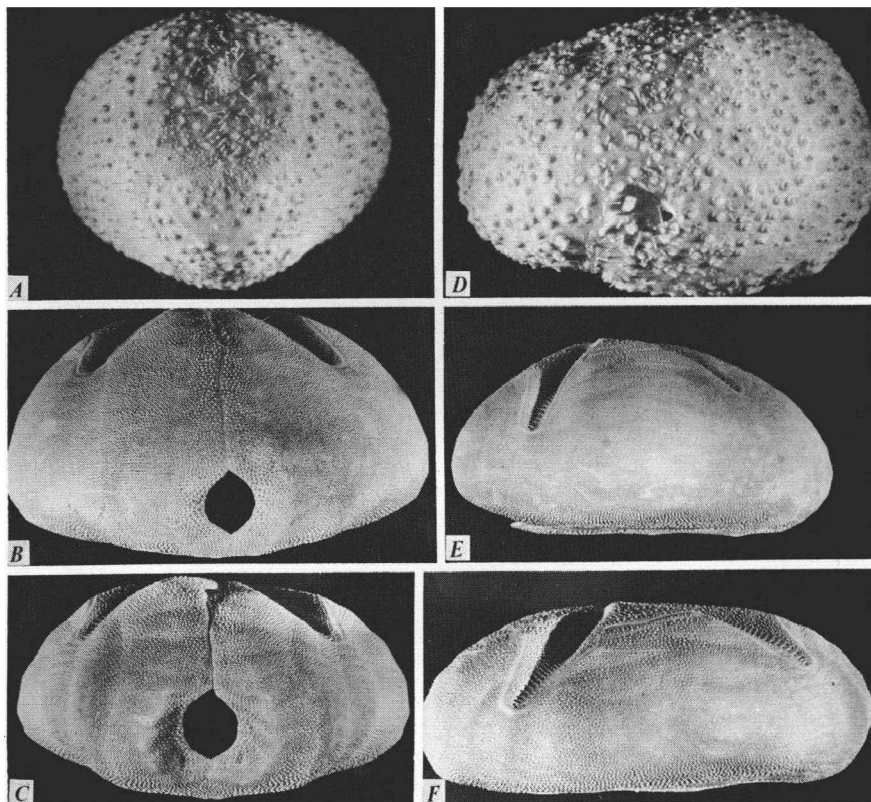


FIGURE 5. Growth and morphological variation in *M. ventricosa* s.s.: A, D, posterior and lateral views of a specimen 7.0 mm long; B, E, same views of a highly arched, broad adult 132 mm long; C, F, same views of a low, narrow adult 142 mm long.

variation. The specimen in Figures 4,B,E, and 5,B,E, is high and broad, whereas that in Figures 4,C,F, and 5,C,F, is low and narrow. Variation in degree of flexion of the anterior paired petals is also evident from a comparison of these two specimens, as is the relative position of the peristome and the width of the plastron.

*M. ventricosa* s.s. grows rapidly as a juvenile, reaches adult size within two years, and a maximum size within four years (Chesher, 1969). After three or four years, growth apparently stops and the test becomes thicker and stronger. During growth, the relative proportions of many features of the test change, so juvenile urchins are markedly different from adults. Table 2 and Figures 2, 3, and 4 indicate the morphological changes of *M.*

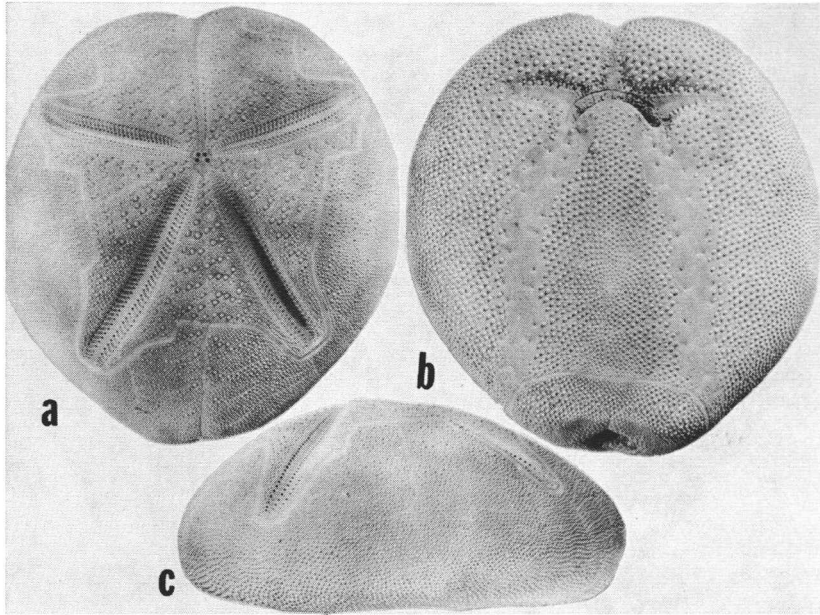


FIGURE 6. *Meoma ventricosa grandis* (test length 114 mm), Acapulco, Mexico: a, dorsal view; b, ventral view; c, lateral view.

*ventricosa* s.s. during growth. The most striking changes (as pointed out by Kier & Grant, 1965) are the changes in the general shape of the test, the increase in the proportional length of the posterior petals, and the loss of the portion of the subanal fasciole nearest the periproct.

Coloration varies considerably during growth. Young specimens are white. During growth, pigmentation increases by the accumulation of a reddish brown pigment, and many adult specimens are almost black. Specimens from shallower, silted areas are darker than those from deeper water. Specimens from these shallower areas also tend to be smaller, and to have a coarser tuberculation than those from deeper water (Chesher, 1969).

Specimens from Santa Marta, Colombia, from Jamaica, and from Bermuda were compared to the "average" Florida population. All characters listed in Table 2 were within one  $S_{y \cdot x}$  or one S.D. of the expected values for given test lengths except the width of the plastron. The width of the plastron was slightly lower than expected in the Colombian specimens (significant at the 90 per cent level) and much higher than expected (significant at the 99 per cent level) in the Bermudan specimen. There appears to be a cline in this character such that the plastron becomes broader, proportionally, in specimens from more northerly locations. For all other char-

TABLE 3  
STATISTICAL SUMMARY: *Meoma ventricosa grandis*\*  
(Abbreviations from Figure 1 and section on abbreviations)

SECTION 1: Characters expressed as percentages of the test length					
Character	Mean	S.E.	S.D.	Range	C.V.
ax	38.02	0.36	1.62	34.65-40.59	4.25
lf	28.63	0.414	1.85	25.00-32.00	6.47
SECTION 2: Characters ( $Y$ in mm) expressed as $\log_e Y = a + b(\log_e X)$ , where $X$ = test length in mm; S.D. $\log_e X = 0.0934$ ; and Mean $\log_e X = 4.6556$					
Character	$a$	$b$	$S_{y..x}$	$r$	
ap	-0.9979	1.0440	0.035	0.93943	
pp	-1.3382	1.1354	0.044	0.91890	
pw	-1.3659	0.9327	0.047	0.87457	
ppfl	0.0308	1.2459	0.033	0.96096	
ae	-0.3038	1.0051	0.023	0.97065	
pe	-0.7870	1.0227	0.047	0.89458	
safd	-3.9000	1.3985	0.116	0.74002	

## SECTION 3: Plates on which fascioles occur

	III b	3		IV a	4		V a	5 a
		a	b		a	b		
Peripetalous fasciole	9	5	5-7	14-15	8-10	9-10	17-18	12-13
Subanal fasciole	—	—	—	—	—	—	6-9+	3

## SECTION 4: Number of feeding tube-feet in series b of phyllode IV = 8 to 10

\* N = 20 specimens. Location as given under Material Examined.

acters the variation within Florida populations was greater than the variation from the extremes of the geographic range.

Abnormalities, such as the occurrence of respiratory tube-feet in ambulacrum III, and pedicellariae, are described elsewhere (Chesher 1969).

*Meoma ventricosa* (Lamarck, 1816) *grandis* Gray, 1851

Fig. 6; Tables 1, 3

*Meoma grandis* Gray, 1851: 132.—Mortensen, 1951: 526, pl. 36, figs. 2-6, pl. 62, figs. 2-5, 7, 8, 11, 13, 14 (syn. complete).—Caso, 1953: 222.—Mayr, 1954: 6.—Hyman, 1955: 548.—Madsen, 1957: 476.—Caso, 1961: 300, fig. 124.—Fischer, 1966: U592.

*Macropneustes grandis*, Cooke, 1959: 83.

*Material Examined*.—14 specimens, 95.5 to 121 mm TL, Acapulco, Mexico; M.C.Z. 3162.—1 specimen, 89.4 mm TL, Manzanillo, Mexico,

40 m; M.C.Z. 6068.—2 specimens, 90 to 98.4 mm TL, Choco, Pt. Utria, Colombia, 30 m; M.C.Z. 7497.—1 specimen, 101 mm TL, Santa Inez Bay, Gulf of California, 40 m; M.C.Z. 7367.—1 specimen, 105 mm TL, Conception Bay, Gulf of California; M.C.Z. 7647.—1 specimen, 95.4 mm TL, Port Guatulco, Mexico, 20 m; M.C.Z. 7648.

*Diagnosis*.—Aboral portion of the subanal fasciole degenerate in adults, peripetalous fasciole crossing plate 9 or 10 (IIIb); peristome larger than 13 per cent TL and with more than 6 pores in series b of phyllode IV; color dark brown to black, distance from lower portion of periproct to the adoral portion of subanal fasciole usually less than the vertical diameter of the periproct.

*Description*.—When measurements of 20 specimens (89 to 121 mm TL) of this Pacific subspecies were compared to those for the population of *M. ventricosa* s.s. from Florida, only two characters varied significantly. These were the distance from the lower portion of the periproct to the adoral portion of the subanal fasciole (safd) and the distance from the apical system to the lateral portion of the peripetalous fasciole (lf). These two characters show no ecological variation and probably represent the best characters for separating the two subspecies. The specimens from the Pacific coast of Colombia are not, however, significantly different from the specimens of the Atlantic subspecies in these characters. One of the two specimens, in fact, has measurements which are almost the same as would be expected for a specimen of *M. ventricosa* s.s. of a similar size. The other specimen and the specimens from Mexico and the Gulf of California are more distinct. All those from the northernmost portion of the distribution in the Pacific are significantly different (99 per cent level) from the specimens of the Atlantic subspecies. There thus appears to be a character cline in these two characters in the Pacific subspecies, with the specimens from the south closely resembling those of the Atlantic subspecies.

As pointed out by Mortensen (1951), the spines appear coarser and the pigmentation darker in the Pacific subspecies than in the Atlantic subspecies. It has been shown (Chesher, 1969) that these characters are subject to ecological variation and may occur in *M. ventricosa* s.s. from silty, shallow-water habitats.

Some of the characters of *M. ventricosa grandis* are summarized in Table 3. All measurements presented in the table of characteristics for *M. ventricosa* s.s. were taken, but only those characters which showed some degree of difference from *M. ventricosa* s.s. are presented.

*Holotype*.—*Meoma grandis*, British Museum (Natural History) number 1949.10.24.6.



TABLE 4

MEASUREMENTS (MM) OF THE SPECIMENS OF *Meoma cadenati* AND *M. frangibilis* COMPARED TO THE MEAN AND 95 PER CENT CONFIDENCE LIMITS OF A SIMILAR-SIZED "AVERAGE" SPECIMEN OF *M. ventricosa* s.s.

(Those characters which fall outside the 95 per cent limits of the standard *M. ventricosa* s.s. are underlined)

Character*	<i>M. cadenati</i>	<i>M. frangibilis</i>	<i>M. ventricosa</i> s.s.		
			Mean	Lower limit	Upper limit
tl	132	130	130		
ap	57.5	<u>45.0</u>	54.2	46.9	62.7
pp	61.2	<u>57.5</u>	60.1	51.8	69.8
pl	48.0	<u>59.2</u>	51.4	47.0	56.2
d	<u>48.0</u>	<u>42.1</u>	38.9	35.0	43.2
ae	<u>87.6</u>	78.0	87.2	77.4	98.2
pe	59.2	<u>53.0</u>	62.0	55.3	69.4
pap	<u>36</u>	<u>37</u>	41	37	45
ppp	<u>34</u>	42	43	39	48
safd	<u>31.0</u>	<u>25.0</u>	20.3	17.3	23.9
pw	<u>16.5</u>	<u>16.2</u>	20.8	17.4	24.9

\* Abbreviations from Figure 1 and section on abbreviations.

*Type-Locality*.—Acapulco, Mexico (locality uncertain, A. M. Clark, personal communication, 1969).

*Discussion*.—It can be assumed that, prior to the uplifting of the Central American land bridge, *Meoma ventricosa* formed a large, transoceanic population. These populations were separated into Atlantic and Pacific components by the closing of the Panamic seaway in northern Colombia during the Pliocene (Woodring, 1965; Lloyd, 1963). The two populations have, therefore, been isolated for more than a million years. Since the specimens of *M. ventricosa grandis* from the northern portion of the present range show the greatest amount of divergence from the Atlantic stock, it is possible that they had begun differentiating even before the uplifting of the land bridge. The specimens of *M. ventricosa* from the Atlantic and Pacific coasts of Colombia are much more closely related, and it is doubtful that specimens from these two localities could be separated with more than 75 per cent accuracy. If a Panamic sea-level canal is built (Rubinoff, 1968) and the two populations are united, it would be extremely difficult to distinguish with certainty the origin of any particular specimens, especially if the canal is constructed in Colombia. Should the two populations freely interbreed, it would be impossible, with the existing information, to identify hybrids.

TABLE 5  
MEASUREMENTS (IN MM) AND OTHER DATA FOR CHARACTERS OF *Meoma*  
*cadenati* AND *M. frangibilis*  
(Abbreviations from Figure 1 and section on abbreviations)

Character	<i>M. cadenati</i>	<i>M. frangibilis</i>
tl	132	130
tw	114.2	114
h	79.5	59.0
ax	34.8	40.5
pa	20.8	17.6
lp	107.4	104
pw	16.5	16.2
aw	12.2	14.6
ah	16.7	16.3
pl	48.0	59.2
d	48.0	42.1
safw	54.0	55.0
saf1	155	145
ppfl	425	375
ff	49.0	44.0
lf	33.5	25.0
pf	46.5	41.0
ap	57.5	45.0
apw	6.5	8.2
pp	61.2	57.5
ppw	6.6	8.7
ae	87.6	78.0
pe	59.2	53.0
safd	31.0	25.0
pap	36	37
ppp	34	42
Plates on which	IIIb, 7	IIIb, 6
peripetalous fasciole	3a, 5	3a, 4
found:	3b, 5 + 6	3b, 4, 5 + 6
	IVa, 12	IVa, 12
	4a, 8 + 9	4a, 8 + 9
	4b, 9	4b, 9 + 10
	Va, 19	Va, 16
	5a, 13	5a, 12
Plates on which subanal	Vb, 6 to 10	Vb, 6 to 9
fasciole found:	5a, 3 to 6	5a, 3 to 6
Feeding tube-feet in series		
b of phyllode IV	6	6

Despite the million-year isolation, the two geographically isolated populations of *Meoma* have not differentiated sufficiently to be given full specific status. Therefore, the two populations are designated subspecies according to the definition of Mayr *et al.* (1953).

*Meoma cadenati* Madsen, 1957

Fig. 7,d,e,f; Tables 1, 4, 5

*Meoma cadenati* Madsen, 1957: 474, figs. 1-3.

**Material Examined.**—1 specimen, 132 mm TL, Sherbro Island, Sierra Leone, 1953; M.C.Z. 8115.

**Diagnosis.**—A species of *Meoma* with complete subanal fasciole, the peripetalous fasciole crossing plate 7 (IIIb); test strong, anterior paired petals equal in length to posterior petals, longer than 35 per cent TL in adults; plastron width greater than 35 per cent TL in adults.

**Description.**—The measurements of the various features of the test are given in Table 4. Figure 7, d-f, shows the overall features of the test, which is light brown and quite robust.

This species differs from the other species and subspecies of *Meoma*, as pointed out in the key to the species and in Table 1. Measurements of *M. cadenati* are compared to those of *M. frangibilis* and *M. ventricosa* s.s. in Table 5. Only one other specimen of this species is known: the holotype. According to the description and figures of Madsen (1957), the two specimens are alike in the key characters.

When measurements of the single specimen were compared to those for the "standard" Floridian population of *M. ventricosa* s.s., six characters were found which were significantly (99 per cent level) different. The method of comparison was that outlined by Simpson *et al.* (1960:205-212). This method assumes conformity in the variability of the considered characters in the two populations. That such conformity exists can be seen by comparing the coefficient of variation in the Floridian populations to similar coefficients derived for other shallow-water and deep-water brissids. Thus the coefficient of variation of the distance from the apical system to the anterior portion of the test (ax) is 5.5 for *M. ventricosa* s.s., 4.25 for *M. ventricosa grandis*, 5.4 for *Plagiobrissus grandis* (Chesher, unpublished data) and 5.4 for *Brissopsis alta* (Chesher, 1968). It is relatively safe to assume, therefore, that the population of *Meoma cadenati* will have a coefficient of variation close to 5 for the same character.

In the African specimen, the apical system is 26.4 per cent of the test length from the anterior end of the test. Based on the statistics in Table 2, a Floridian specimen of *M. ventricosa* s.s. of similar size would have the apical system situated  $38.8 \pm 2.14$  per cent from the anterior of the test (significant at the 99 per cent level). Clearly, the location of the apical system is significantly more anterior in the African species.

The plastron is 48 mm wide in the African specimen, whereas a specimen of *Meoma* of similar size in Florida would have a plastron 38.9 mm wide with a range at the 95 per cent level of 35 mm to 43 mm. The pore-

pairs (pap) in the petaloid region of IVb number 36 in the African specimen, and thus are fewer than in a 132-mm Floridian specimen ( $41 \pm 2$  pore-pairs; significant at the 98 per cent level). Similarly, the number of pore-pairs (ppp) of the posterior petal Va is below that expected for a Floridian specimen (34 as opposed to  $43 \pm 2.3$  pore-pairs; significant at the 99 per cent level). There is a complete subanal fasciole in the African specimen, a situation which was found in only two specimens out of many hundreds examined of the western Atlantic species. The peripetalous fasciole crosses plate 7 (IIIb), as opposed to 10-12 (IIIb) in the Floridian specimens; and plate 12 (IVa), as opposed to plates 14-15 (IVa) in the Floridian specimens.

*Holotype*.—138 mm TL, Institut Français d'Afrique Noire.

*Type-Locality*.—South of Dakar, Sénégal, 100 m.

***Meoma frangibilis*, n. sp.**

Figs. 7, a-c, 8; Tables 1, 4, 5

*Material Examined*.—1 specimen, 130 mm TL, Bay of Panama, R/V PILLSBURY Sta. 549,  $7^{\circ}59.5'N$ ,  $78^{\circ}30.3'W$ , 55 m, May 1967.

*Diagnosis*.—A species of *Meoma* with complete subanal fasciole, the peripetalous fasciole crossing plates 6 (IIIb) and 4 (3a); test thin, fragile; anterior paired petals short (less than 35 per cent TL in adults); plastron width less than 35 per cent TL in adults.

*Description*.—Measurements of various features of the test are given in Table 4, and Fig. 7, a-c shows the general shape of the test. The plates are exceedingly fragile (hence the name *frangibilis*) and when cleaned with NaOH reveal a light purple color.

Ambulacrum III is slightly sunken from the apical system to the peristome, forming a moderately deep notch in the anterior ambitus. The small, single pores of the sensory tube-feet are widely spaced and usually have one or two small tubercles (spines) between them. The interporiferous zone is broad and granular. The phyllode of III is poorly developed, with only four feeding tube-feet per series. The peripetalous fasciole crosses IIIb on plate 6.

The peripetalous fasciole crosses ambulacrum IVa on plate 12. The plates outside the peripetalous fasciole are covered with irregular tuberculation in ambulacra II and IV, and only the interporiferous zone of the phyllodes is naked. There are six feeding tube-feet in the posterior series of the phyllodes, and seven in the anterior series. The petaloid portion of the anterior paired ambulacra are narrow, straight, and moderately sunken, with the interporiferous zone naked and about the same width as a pore

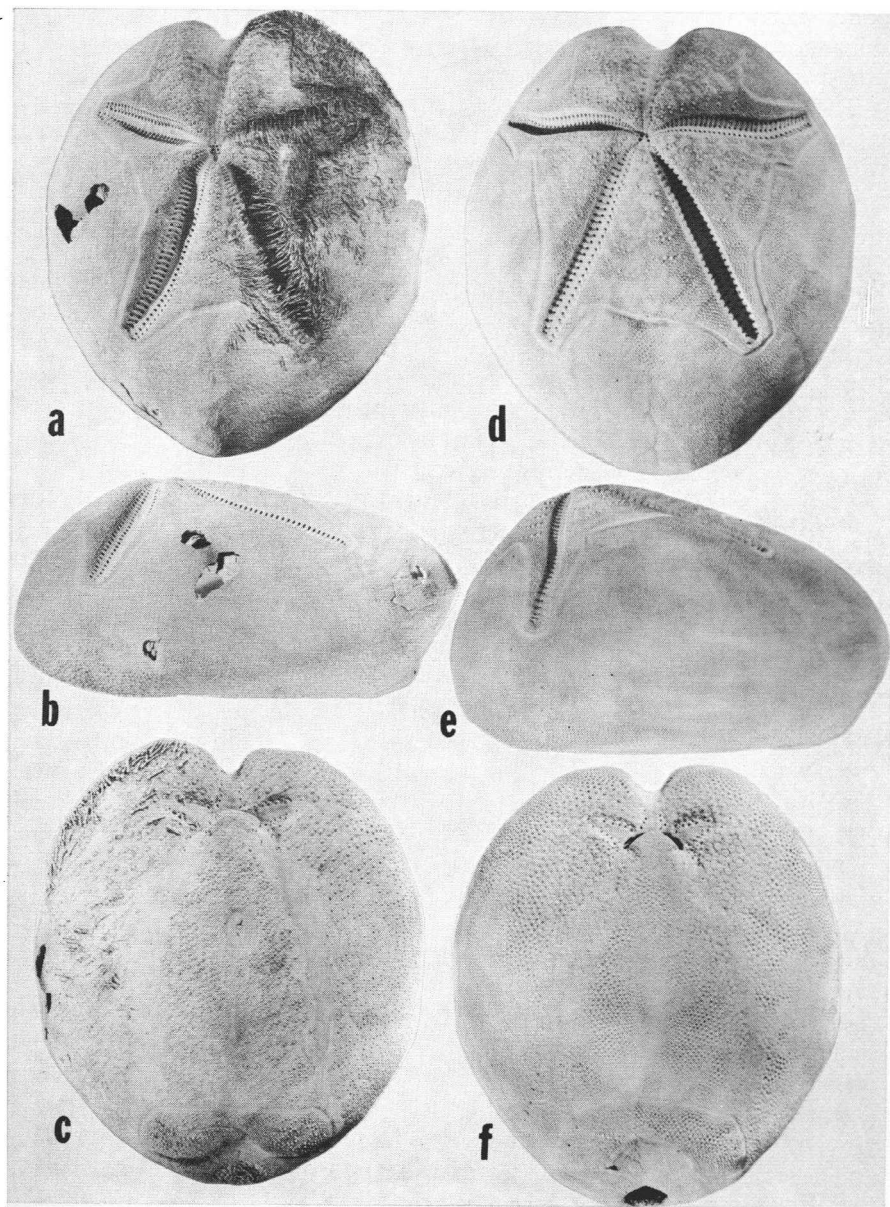


FIGURE 7.—a-c, *Meoma frangibilis*, holotype: a, dorsal view; b, lateral view; c, ventral view.—d-f, *Meoma cadenati* (test length 132 mm), Sherbro Island, Sierra Leone: d, dorsal view; e, lateral view; f, ventral view.

zone. There are 33 fully developed respiratory pore-pairs in the posterior pore-series of IV, the four nearest the apical system being quite small. Each pore-pair is separated by a ridge crested by a row of tubercles.

The peripetalous fasciole crosses ambulacrum Va on plate 16. The plates outside the peripetalous fasciole in ambulacra I and V are covered with irregular tuberculation to plate 9 of the posterior plate series. There is a naked, granular zone on the median ambulacral area from the peristome to plate 9. Three feeding tube-feet are located in each series of the posterior phyllodes. Within the subanal fasciole, each ambulacrum has three well-developed subanal tube-feet with double pore-pairs. Ambulacral plates 6, 7, 8, and 9 of the posterior series are adproctally extended and included within the subanal fasciole. The petaloid portions of the posterior paired ambulacra are moderately sunken and slightly curved. They are longer than the anterior petals (the latter being 78.4 per cent of the posterior petals), and have 36 fully developed and 6 partly developed pore-pairs in the anterior pore-series of each petal.

Secondary spines are irregularly scattered over the interambulacra and are of a small, uniform size. These spines (and their tubercles) are slightly larger near the peristome and within the peripetalous fasciole. Within the peripetalous fasciole are some small primary spines, which are best developed in IA 2 and 3. Tertiary spines form a dense coat between the secondary spines and are thin and hairlike. There are no naked areas in the interambulacra.

The plastron and epiplastron are as usual for the genus, but the areas within the bilobed subanal fasciole are more inflated than usual in *Meoma* (Fig. 7, b). The labrum does not extend past the first ambulacral plates.

Plates 5, 6, 7, and 8 enclose the anal system, which is vertically oval and placed high on the obliquely truncated posterior end to the test.

The peripetalous fasciole is sinuous, broad (averaging 1.7 mm in width), and clearly defined. It crosses plates 6 (IIIb); 4 (3a); 4, 5, 6 (3b); 12 (IVa); 8, 9 (4a); 9, 10 (4b); 16 (Va); and 12 (5a). The subanal fasciole is bilobed, broad (averaging 1.1 mm in width), and clearly defined. It crosses plates 6, 7, 8, 9 (Vb) and 3, 4, 5, 6 (5a).

Figure 8 shows the various types of pedicellariae found. They are not significantly different from those of other species of *Meoma* to be considered diagnostic. Only long and short forms of tridentate pedicellariae, triphyllous and rostrate pedicellariae were found. Globiferous pedicellariae were absent, but may, as in the other species, be present in young specimens.

The color of the dried specimen is light brown. When cleaned with bleach, the test becomes a light violet color.

The dried intestine was still present inside the test and showed an arrangement of siphons and haemal vessels similar to that found in *M. ventricosa* (Chesher, 1969). The intestine was full of a silty, brown sand. Some

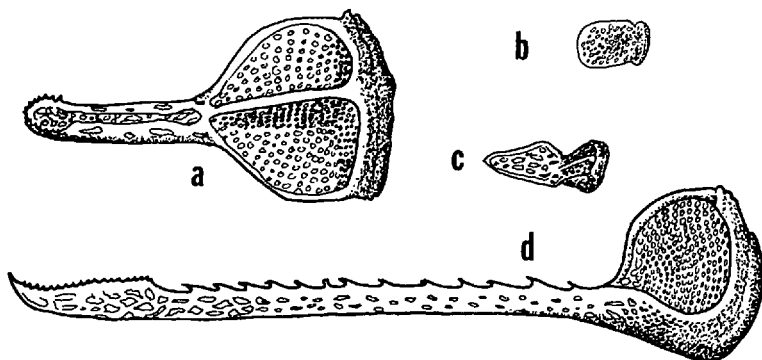


FIGURE 8. Pedicellariae of *M. frangibilis*: a, rostrate valve 0.54 mm long; b, triphyllous valve 0.11 mm long; c, tridentate valve 0.20 mm long; d, tridentate valve 1.13 mm long.

surprisingly large objects were found in the intestine. One pelecypod shell  $11 \times 10 \times 4.2$  mm and a cidarid spine  $23 \times 1.5$  mm were found within the gut. Undoubtedly, this species is a general, nonselective bottom feeder, ingesting the sand as it moves along, as does *M. ventricosa* (Chesher, 1969).

*Holotype*.—130 mm TL, M.C.Z. 8207. The only known specimen.

*Type-Locality*.—Bay of Panama, R/V PILLSBURY Sta. 549,  $7^{\circ}59.5'N$ ,  $78^{\circ}30.3'W$ , 55 m, fine, heavily silted, brown sand.

*Commensals*.—Unidentified erycinacean bivalves (probably *Montacuta*) were attached by their byssal threads to various parts of the test, particularly in the petaloid areas. Specimens still remain in the right paired petals.

#### EVOLUTION

The only fossil species which Mortensen (1951) considered congeneric with *M. ventricosa* was *M. antiqua* Arnold & Clark 1927, of unknown age from Jamaica. Durham (1950) described a *Meoma* sp. from the lower Pliocene of the Gulf of California and Roig (1952) described *M. caobaensis* from a poorly preserved specimen from the Eocene of Cuba.

It is evident that *M. ventricosa* is closely related to *M. cadenati*, and that *M. cadenati* is related to *M. frangibilis*. A continuous series in gross morphological change is, in fact, evident from *M. ventricosa grandis* to *M. ventricosa* s.s., to *M. cadenati*, and to *M. frangibilis*. *M. frangibilis*, however, is not very similar to *M. ventricosa grandis*, and if the intermediate forms were not present, the two species would have been classified as distinct genera. *M. frangibilis* would have been considered a *Peripneustes* (=

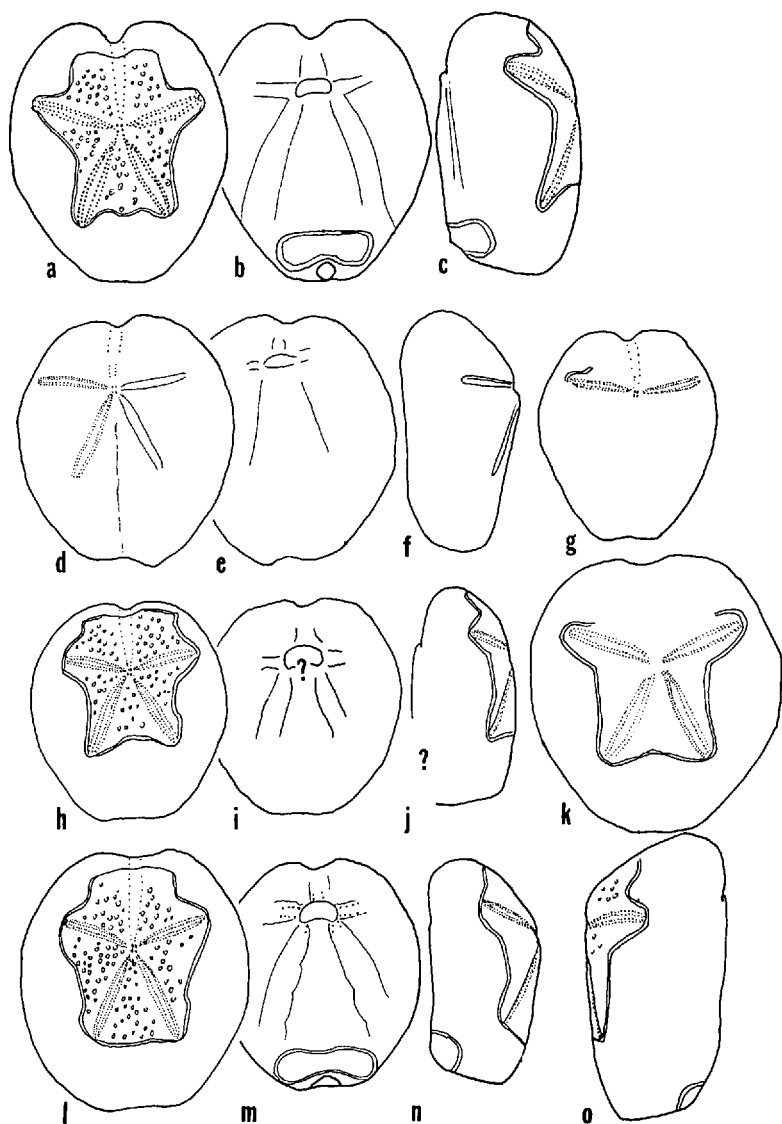


FIGURE 9. Fossil species of the genus *Meoma*: a-c, *Peripneustes clevei* Cotteau, 1875 (pl. 7, 4-7); d-f, *Schizobrissus kewi* Durham, 1961 (pl. 67, text-fig. 2c); g, *Macropneustes dubius* Israelsky, 1924; h-j, *Macropneustes biarritzensis* Cotteau, 1885 (pl. 49); k and o, *Brissus declivis* Herklots, 1854 (pl. 3); l-n, *Macropneustes pellati* Cotteau, 1885 (pl. 85).



*Schizobrissus*) as it is similar to the Eocene *P. antillarum* Cotteau (see Mortensen, 1951: text-fig. 227). When various species of fossil *Peripneustes* (many originally classified as belonging to the genus *Macropneustes*) were examined, it became apparent that a continuum exists between the various forms of *Peripneustes* and the Recent *Meoma*.

The nomenclature of the genus *Peripneustes* requires some consideration. Cotteau (1875) originated the genus *Peripneustes* for the species *P. antillarum* and *P. clevei*. Lambert & Thiéry (1924) placed these species, as well as *M. biarritzensis* (Cotteau) and several other species in the genus *Schizobrissus* Pomel, 1869. Pomel created the genus *Schizobrissus* for *Brissus cruciatus* Agassiz, a species known from the anterior portion of a single Miocene specimen. In 1883, he stated, "Le type [of *Schizobrissus*] est *S. mauritanicus* Pom. du terrain miocene, ainsi que le *S. cruciatus* (Ag. sub *Brissus*)." Lambert & Thiéry (1924) correctly pointed out that *S. cruciatus* must remain the type of the genus. Probably, Pomel attempted to change the type-species because of the lack of definitive characters on the fragment on which he had based the name. There is no way of knowing what the fragment represents (or even that it is a brissid), but its depressed form, short petals, and general appearance show no clear relationship with Cotteau's species. It would be incorrect to synonymize *Schizobrissus* with *Meoma*. Instead, *M. antillarum*, *M. biarritzensis*, and *M. clevei* are removed from *Schizobrissus* as representatives of the genus *Meoma*.

*Schizobrissus jacksoni* Lambert is, as Mortensen (1951) pointed out, based on Jackson's (1922) pl. 15, fig. 1 of *Macropneustes antillarum*. Re-examination of this specimen (U.S.N.M. 115369), a paratype of Cotteau's species, showed little basis for considering it different from *M. antillarum*.

*Meoma pellati* (Cotteau) was described as a *Macropneustes* and placed in *Dekia* by Lambert & Thiéry, an action which Mortensen (1951) correctly described as "rather arbitrary." *Meoma declivis* (Herklots) was described as a *Brissus* and placed in the genus *Meoma* by Lambert & Thiéry.

Table 6 summarizes the various species of *Meoma* found in the fossil record, and some of these are illustrated in Figure 9.

There are several other species which are not listed here that could be representative of *Meoma* but these are so poorly preserved, described, or figured that nothing can be determined about their relationships. These additional species would not, however, alter the gross evolutionary picture of the genus.

Several species are described from the Eocene of Europe, which represent intermediate stages in the evolution of *Meoma* from *Macropneustes*. This does not mean that *Meoma* and *Macropneustes* are synonymous as inferred by Cooke (1959). Obviously, one could synonymize all genera if the fossil history were sufficiently well known. Available data indicate

TABLE 6  
FOSSIL SPECIES OF THE GENUS *Meoma*  
(Illustrated in Figure 9)

Species	Time	Locality	Data from	Specimen examined
<i>Peripneustes clevei</i>	Miocene	Anguilla	Cotteau, 1875	type-material
<i>Peripneustes antillarum</i>	Eocene	Cuba	Cotteau, 1875	type-material
<i>Schizobrissus kewi</i>	Miocene	Costa Rica	Durham, 1961	photograph
<i>Macropneustes dubius</i>	lower Miocene	Mexico	Israelsky, 1924	photograph
<i>Meoma antigua</i>	?	Jamaica	Arnold & Clark, 1927	photograph
<i>Macropneustes biarritzensis</i>	Eocene	France	Cotteau, 1885	drawing
<i>Macropneustes pellati</i>	Eocene	France	Cotteau, 1885	drawing
<i>Macropneustes brissoides</i>	Eocene	France	Cotteau, 1885	drawing
<i>Brissus declivis</i>	Miocene	Java	Herklots, 1854	drawing
<i>Meoma tuberculata</i>	late Oligocene	New Zealand	Hutton, 1873	new specimen
<i>Meoma</i> sp.	Pliocene	Gulf of California	Durham, 1950	photograph

the two genera diverged before, or during, the early Eocene and that both groups existed until the Pleistocene, when *Macropneustes* became extinct. The major differences between the two genera are: the peripetalous fasciole does not indent between the paired petals in the genus *Macropneustes*; and the petaloid areas are not sunken and are similar to those of *Spatangus*, with broad, heavily tuberculated interporiferous zones. The transitional species, which are best left in the genus *Macropneustes*, are *Ma. heberti*, *tumidus*, and *pulvinatus* (see Cotteau, 1885).

The resulting paleontological data offer three useful insights into the evolution of the genus *Meoma*. First, the history of the genus is not American, as might be inferred from the distribution of Recent species, but had its beginnings in the European area. During the late Eocene to Miocene period, the genus *Meoma* existed over a large geographic range, including New Zealand (*M. tuberculata* Hutton, 1873), Java (*M. declivis*, [Herklots, 1854]), and the Americas (*M. antillarum* and *M. clevei* [Cotteau, 1875]). Second, the genus became extinct everywhere except in the Americas

during the late Miocene. Third, the *M. frangibilis-cadenati* group represents the older morphological type, and the *M. ventricosa* group is relatively new, having appeared in the late Miocene or early Pliocene. The *M. ventricosa* group must have been established prior to the uplifting of the Panama land bridge during the Pliocene.

*M. antillarum* is morphologically very similar to the three species from the Miocene of America, *M. clevei*, *M. kewi*, and *M. dubius*. Specimens of *Meoma* have not been found in European strata later than Eocene, and those specimens, while clearly of the genus *Meoma*, do not seem as closely related to the species from the Miocene period of the Americas as does *M. antillarum*. It can be assumed, therefore, that the process which lead to the extinction of the genus from the European seas was complete and that the Eocene species, *M. antillarum*, is ancestral to all the existing species of *Meoma*. Of the three Miocene species, *M. clevei* from Anguilla is closest to *M. antiqua* and *M. ventricosa*. *M. cadenati* and *M. frangibilis* appear to be Recent representatives of the *M. dubius-kewi* group from the Miocene of America. That the African species was not derived from a European ancestor seems evident in the lack of fossil specimens of *Meoma* from Africa, particularly in the vicinity of the Recent populations (Lambert, 1933, 1936, 1937). In addition, European representatives are not known from later than the Eocene.

It is clear from Table 1 that *M. cadenati* has diverged more from *M. frangibilis* than has *M. ventricosa grandis* from *M. ventricosa* s.s. This would indicate that the African form was isolated in the late Miocene or early Pliocene.

The pattern of evolution within the genus appears as a rapid change in an isolated character, followed by long periods of stabilization. In the *M. frangibilis-cadenati* group, the apical system moved closer to the anterior end of the test during the Miocene. Other than this anterior shift in the apical system, which is evident in both *M. kewi* and *M. dubius*, this group closely resembles the Eocene species *M. antillarum*.

In the *M. ventricosa* group, the apical system is similar in position to *M. clevei* and *M. antillarum*. The dorsal portion of the subanal fasciole is lost with age, a character also reported for the fossil *M. antiqua*. Apparently, like the anterior movement of the apical system in the *M. frangibilis-cadenati* group, this character developed only once and has persisted unaltered since that change. There is no evidence of intermediate steps in its development. The number of pores in phyllode IV, series b, is higher in the *M. ventricosa* group than in the older forms. Since this number is the same in both subspecies, which have been separated for over a million years, it can be assumed that this character also changed rapidly and then stabilized. Similarly, the peristome is larger in the *M. ventricosa*

group than in the older forms, and this character has not changed since the uplifting of the Central American land bridge.

The great numbers of *M. ventricosa* and wide distribution throughout tropical America demonstrate that this form is more successful than the old form represented by *M. frangibilis*. It is interesting to note, however, that the older form still survives within the same geographic area.

#### SUMMARY

Study of a new species of *Meoma*, *M. frangibilis*, collected from the R/V PILLSBURY in the Bay of Panama, has lead to clarification of the relationship of the Recent species of *Meoma* with fossil forms. The genus *Peripneustes* Cotteau, previously synonymized with the genus *Schizobrissus* Pomel, must now be removed from that genus and synonymized with the genus *Meoma*. The status of *Schizobrissus* is unknown. The Recent species of *Meoma* are probably derived from the Eocene species *M. antillarum* (Cotteau). The genus evolved from a *Macropneustes* ancestor in the Eocene of Europe. The geographic distribution of the genus, during the Miocene, extended from New Zealand to Central America. *Meoma* apparently became extinct everywhere but in the Americas during the Miocene. The African species *M. cadenati* probably was a late Miocene or early Pliocene immigrant from America.

The pattern of evolution within the genus is one of rapid change followed by long periods of stabilization, as evidenced by the few changes that have occurred during the past million years in the subspecies of *M. ventricosa* isolated by the Central American land bridge.

#### SUMARIO

#### EVOLUCIÓN EN EL GÉNERO *Meoma* (ECHINOIDEA: SPATANGOIDA) CON DESCRIPCIÓN DE UNA NUEVA ESPECIE DE PANAMÁ

Una nueva especie de *Meoma*, *M. frangibilis*, colectada en la bahía de Panamá por el barco de investigaciones PILLSBURY, aclara las relaciones de las especies recientes de *Meoma* con las formas fósiles. El género *Peripneustes* Cotteau debe ser retirado del género *Schizobrissus* Pomel y hacerse sinónimo de *Meoma*. La posición de *Schizobrissus* es desconocida. Las especies recientes de *Meoma* se derivan probablemente de la especie del Eoceno *M. antillarum* (Cotteau). El género evolucionó de *Macropneustes*, un antecesor en el Eoceno de Europa. La distribución geográfica del género se extendió durante el Mioceno desde New Zealand hasta América Central. Aparentemente durante el Mioceno *Meoma* se extinguió en todas partes menos en América. La especie africana *M. cadenati* probablemente immigró de América al final del Mioceno o principios del Plioceno.

El patrón de evolución en el género es de cambio rápido seguido de largos períodos de estabilización como se evidencia por los escasos cambios que han ocurrido durante el último millón de años en la subespecie de *M. ventricosa* aislada por el puente terrestre de América Central.

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